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Limits to the co-occurrence of avian herbivores. How geese share scarce resources.

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Abstract

This thesis brings together studies on the performance of highly social avian herbivores, brent *Branta bernicla bernicla* and barnacle geese *Branta leucopsis* operating in a patchy environment. Numbers identify the chapter. The introductory chapter (1.) is not included in the abstract.

2. Observations on a marked breeding population of the barnacle goose on Spitsbergen (Ny-Ålesund, 78°55'N, 11°56'E) elucidated the impact of predation risk on habitat use during brood-rearing by contrasting two seasons accompanied by local absence of the polar fox, *Alopex lagopus*, with a season marked by frequent incursions of foxes. In the fox-year the goose families were restricted to lakeshore sites offering safety but poor in forage plants compared to the upland tundra utilised in 'safe' years.

3. In the same study site an enrichment experiment was performed by fertilising small plots on the tundra frequently used by a flock of moulting non-breeding barnacle geese. Earlier a dominance hierarchy had been established by observation of aggressive encounters between flockmates. Dominance was best described by age and sex-specific body mass. When the enriched patches were opened, subordinate individuals were the first to find them, but were quickly displaced by more dominant geese that then monopolised the bonus food. On subsequent flock passages the enriched patches were preferentially grazed by individuals initially succeeding in feeding there. Females returning the next year had enjoyed a higher dominance status the previous season than those failing to return.

4. Observations on wintering flocks of barnacle geese on the Dutch island Schiermonnikoog (53°30'N, 6°10'E) were facilitated by the high incidence of ringed individuals (relating primarily to the population recently established in Sweden). Successful parents with their young (and sometimes with yearling offspring) claimed positions on the flock edge with first choice of ungrazed shoots, whereas unpaired individuals were over-represented in the low-density central sector. Edge birds were significantly older than those habitually found in the centre and originated from the oldest established colony. Individuals switching between flocks were often unattached birds, but one-third of those immigrants managed to reach preferred edge positions within 3 minutes after landing in the new flock.

Abstract

5. At the Dutch study site, time-activity budgets of geese were recast in energetic terms by obtaining conversion values via non-invasive heart rate loggers applied to captive barnacle and brent geese. This technique of measuring energy expenditure was calibrated individually against oxygen consumption in the laboratory. Daily energy expenditure (DEE) of brent geese in two spring habitats (pastureland and salt marsh, both on the same island) turned out to be closely similar. Including our measurements there are now DEE values for 14 herbivorous anatid species. Their assemblage in a new allometric equation allows the conclusion that this avian group employs a low-cost life style compared to most other birds.

6. By employing the same heart rate technique, the influence of wind exposure, temperature and radiation on the energy expenditure of the two goose species was investigated by exposing captive individuals to natural variation in ambient conditions during winter. These data were integrated in a recently formulated thermoregulation model. Modified for our geese the model explained 42% of the variation in the heart-rate data. It was subsequently employed to calculate expected thermoregulatory costs under various meteorological scenarios, comparing energetic expenditures between microhabitats and between staging sites.

7. Differences in tolerance of salt deposition on marsh plants (the barnacle goose being less tolerant than brent) emerged in a field experiment and matched differences in the mass of the nasal gland responsible for salt excretion (brent having glands heavier by a factor four in relation to metabolic body mass). These findings help explain differential forage utilisation of the two goose species on the salt marsh in spring.

8. Exclosure experiments were performed on the salt marsh of Schiermonnikoog to reveal quality enhancement through previous grazing on swards of *Festuca rubra*, the preferred forage plant for both goose species and the resident brown hare, *Lepus europaeus*, during March through early May. The experiments point to a competitive interaction between hares and geese, and grazing facilitation between barnacle geese (the first to switch to the *Festuca* resource in spring) and brent up to a cut-off point.